

20. DOMINANT AND SUBORDINATE COMPONENTS OF PLANT COMMUNITIES: IMPLICATIONS FOR SUCCESSION, STABILITY AND DIVERSITY

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INTRODUCTION

An accepted research tactic in the analysis of plant and animal communities is to attempt to identify those differences between component species and populations which are likely to minimize competition and permit coexistence. Implicit in this approach is the assumption that resources and/or opportunities for regeneration exist in various forms and in a range of spatial and temporal patterns which are exploited in complementary ways by the constituent species.

In plant communities (at least) this conventional view of niche differentiation and exploitation must be enlarged to accommodate the fact that many communities harbour potential dominants with the capacity to monopolize opportunities for resource capture and regeneration. In all except the most severely disturbed or skeletal habitats it seems likely that the struggle between potential dominants provides a potent driving force for successional change and is a major determinant of the fate of subordinate species. In this chapter it will be argued therefore that studies of dominance should command high priority in our attempts to understand the structure and dynamics of vegetation. It appears necessary not only to analyse the very different mechanisms whereby plants attain dominance but also to identify the factors responsible for the decline and replacement of particular dominants (Watt 1947) and for their debilitation or exclusion from species-rich communities (Al-Mufti *et al.* 1977).

As a corollary we may also seek to understand why many species rarely if ever achieve a dominant status in vegetation. Is the lower relative abundance of such plants within communities a sign that they are perpetual 'also-rans' in the struggle for existence or are there distinct selective advantages associated with playing a subordinate role?

This chapter will attempt to identify some of the essential features of dominant and subordinate plants of terrestrial plant communities and will consider how knowledge relating to them can contribute to our understanding of vegetation characteristics.

DOMINANTS

Dominance implies not only a major contribution to the total biomass of the plant community but the tendency (as an individual or a population) to ramify throughout the edaphic and aerial environments and to influence the identity, quantity and local distribution of the other organisms present. This argument leads to the proposition that dominance mechanisms have two major components.

(a) The mechanism whereby the dominant plant achieves a biomass greater than that of its associates; this mechanism will vary according to the species and habitat conditions.

(b) The effects which dominant plants exert upon the fitness of neighbours; these include deleterious effects (e.g. resource depletion and release of phytotoxins) and promotory effects (e.g. provision of surfaces for epiphytes, release of substrates to parasites, symbionts and decomposing organisms and production of food exploited by herbivores).

These definitions provide for considerable variety in the types of vegetation dominants. The C-S-R model of primary strategies (Grime 1974) permits potential dominants to be distinguished from other plants (Fig. 20.1) and then subdivided into three functional classes which for simplicity are described respectively as ruderal, competitive and stress-tolerant dominants. The differences between these three types of plants are described in Grime (1979) and will not be reviewed in detail here. However, reference to certain of the distinguishing characteristics of the three classes of dominants is essential to an analysis of their role in vegetation dynamics.

Ruderal dominants

Where the vegetation developing in a productive terrestrial habitat suffers frequent and severe destruction it is likely that all of the plant populations present will be too sparse and ephemeral to be capable of exerting dominance as defined under the previous heading. However, where disturbance appears in the form of a single predictable annual event (e.g. winter flooding of river banks, autumn tillage of arable fields), the seasonal cycle may contain an uninterrupted growing season long enough to allow certain annual plants of tall stature and originating by synchronous germination of a large seed population to achieve a biomass sufficient to suppress the performance of neighbouring species. Examples here include *Impatiens glandulifera* on river terraces and crops and weeds of arable land such as *Hordeum vulgare* and *Bromus sterilis*.

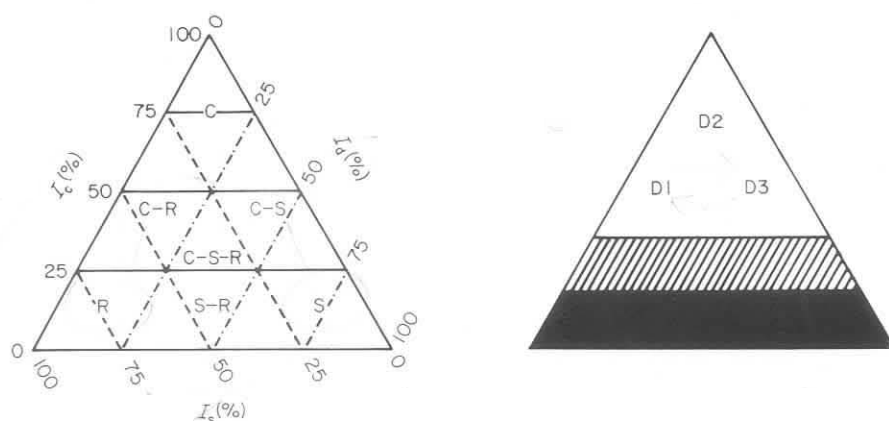


FIG. 20.1 (a) Model describing the various equilibria between competition, stress and disturbance in vegetation and the location of primary and secondary strategies. C, competitor; S, stress-tolerant; R, ruderal; C-R, competitive-ruderal; S-R, stress-tolerant-ruderal; C-S, stress-tolerant-competitor; C-S-R, 'C-S-R strategist'. I_c , relative importance of competition (—); I_s , relative importance of stress (· · ·); I_d , relative importance of disturbance (---). (b) The distribution of three floristic elements within the triangular model: (□) potential dominants; (■) plants highly adapted to extremely disturbed and/or unproductive conditions; (▨) subordinates. D1, ruderal dominants; D2, competitive dominants; D3, stress-tolerant dominants.

Competitive dominants

In circumstances where productive habitats are subjected to occasional catastrophic disturbance (e.g. sites experiencing floods or fires every 5–30 years) the intervals during which vegetation recovery occurs are long enough to allow development of a rapidly-expanding biomass monopolized by herbs (e.g. *Urtica dioica*, *Reynoutria japonica*), shrubs (e.g. *Sambucus nigra*, *Piper hispidum*) and trees (e.g. *Populus grandidentata*, *Cecropia obtusifolius*) with high relative growth rates. Three features of competitive dominants ('active foraging', covariance in competitive abilities and life-form diversity) deserve special comment since they have profound implications for ecological theory.

'Active foraging'

Competitive dominants achieve high rates of resource capture in productive environments by means of exceedingly dynamic root systems and leaf canopies. From year to year, and in most cases within each growing season,

there is continuous replacement of the leaves and roots. This feature, coupled with the rapid morphogenetic responses of expanding leaves and roots to local patchiness in resource concentration (Grime 1979; Crick 1985) results in a continuous adjustment of the spatial distribution of the absorptive surfaces above and below ground. This ability to maintain leaves and roots in the resource-rich zones of a changing environment is of key significance in the success of early successional perennials of productive habitats since it explains the ability of these dominants to sustain high rates of resource capture, growth and reproduction despite the development of local zones of resource depletion originating from the activity of the dominant itself and from encroachments by neighbours.

It is clear that the costs involved in such active foraging for light energy, mineral nutrients and water are considerable in terms of the high rates of reinvestment of captured resources in the construction of new leaves and roots and in their rapid senescence. To these costs we must add those associated with the high rates of herbivory experienced by the weakly-defended tissues of many competitive dominants (for evidence of this phenomenon and an evolutionary explanation for it see Grime 1979, Coley 1983). We may suspect, therefore, that there are severe penalties attached to active foraging by early successional dominants; the significance of these will be explored later in this paper.

Covariance in competitive abilities

The resources for which autotrophic plants compete are numerous (light energy, water and various mineral elements) and they are often located in different parts of the plant's environment. This has prompted some ecologists, most notably Newman (1973, 1983), to suggest that a distinction should be drawn between plants which compete effectively for light in the dense vegetation of fertile relatively undisturbed sites and those which occupy unproductive habitats and might be supposed to have superior competitive ability for below-ground resources. This view has been contested (Grime 1973b; Mahmoud & Grime 1976; Chapin 1980), with the argument that successful competition in productive vegetation depends upon simultaneously high rates of capture of light, water and mineral nutrients under circumstances in which zones of resource depletion are developing both above and (less conspicuously) below ground.

Evidence of the strong interdependence of competitive abilities above and below ground is available from a recent experiment in which turf microcosms providing localized access to subsoil moisture and growing under high and low soil fertility were subjected to 7 days of drought. The results (Fig. 20.2) show consistent differential mortality among the twenty

species of herbaceous plants established in the microcosms. Fatalities were considerably higher in the more productive turf, presumably as a result of the larger transpiring shoot biomass. Of more critical interest, however, is the fact that at both high and low fertility the pattern of drought mortalities among the species was directly correlated with an index of competitive dominance (Grime 1973a) based upon above-ground attributes (height, lateral spread and litter accumulation) of the plant. This strongly suggests that species such as *Dactylis glomerata* and *Festuca rubra* owe their success in productive habitats not only to monopoly of the aerial environment but also to the capacity for extensive exploration and effective resource capture below ground.

Life-form diversity

Active foraging and high rates of resource capture and growth do not necessarily confer the potential for vegetation dominance. Ruderal dominants such as those described on p. 414, and even many small ephemeral weeds, exhibit active foraging and high rates of resource capture but they rapidly succumb when exposed to competition by large perennial plants. Failure here can be attributed to the diversion of captured resources to seeds rather than into the construction of the matrix of robust vegetative

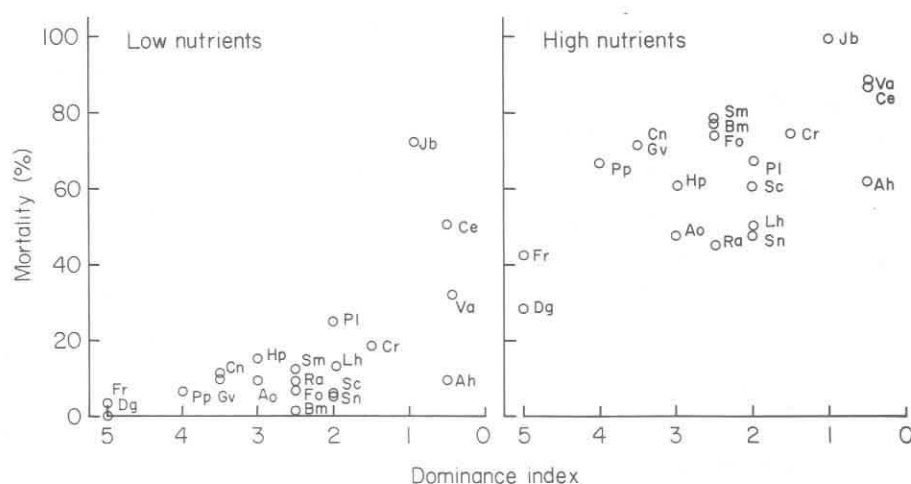


FIG. 20.2 A comparison of drought mortalities in twenty herbaceous species established in nutrient-poor (left) and nutrient-rich (right) microcosms. Ah, *Arabis hirsuta*; Ao, *Anthoxanthum odoratum*; Bm, *Briza media*; Ce, *Centaurea erythraea*; Cn, *Centaurea nigra*; Cr, *Campanula rotundifolia*; Dg, *Dactylis glomerata*; Fo, *Festuca ovina*; Fr, *Festuca rubra*; Gv, *Galium verum*; Hp, *Hieracium pilosella*; Jb, *Juncus bufonius*; Lh, *Leontodon hispidus*; Pl, *Plantago lanceolata*; Pp, *Poa pratensis*; Ra, *Rumex acetosa*; Sc, *Scabiosa columbaria*; Sm, *Sanguisorba minor*; Sn, *Silene nutans*; Va, *Veronica arvensis*.

tissues necessary for exclusive occupation of an undisturbed site over an extended period. This exemplifies the principle that dominance depends not merely upon resource acquisition but upon the way in which captured resources are utilized by the plant. Hence, from the experimental studies of Mahmoud & Grime (1976) and Crick (1985) we may deduce that the ability of the common grass *Arrhenatherum elatius* to dominate extensive areas of productive derelict grassland in Europe is not attributable solely to rapid rates of resource capture and growth, since many other common grasses are superior in these respects (Grime & Hunt 1975; Crick 1985). Rather it would appear that dominance by *A. elatius* is related to additional features such as the capacity to develop massive persistent tussocks which are impenetrable by other species. This same concept is highly relevant to our understanding of the life-form diversity in the sequence of competitive dominants (perennial herbs—shrubs—trees) often observed during the early stages of secondary succession in productive habitats in temperate regions. Accepting the argument of Egler (1954), many of the woody plants which eventually displace the herbaceous perennials originate from seedlings present at the early stages of recolonization. This suggests that the most likely explanation for the delayed dominance by woody species is the result of three factors. The first is the longer period required for the development of the elevated leaf canopies of trees and shrubs. The second is the slower growth rates due to the production of wood at the expense of leaves and roots. The third factor is the suppression of woody seedlings by the herbaceous dominants which, through extensive lateral spread above and below ground, are better equipped to dominate in the short-term. It is interesting to note that in tropical forests herbaceous dominants are often less conspicuous in the early stages of secondary succession; this observation may be related to the fact that here many of the pioneer trees of disturbed sites delay the development of wood until the late sapling stage and produce seedlings with multiple stems which allow lateral spread of the leaf canopy at a very early stage of development.

Stress-tolerant dominants

Earlier in this paper it was suggested that ecological penalties are associated with the active foraging mechanisms of competitive dominants. These may be expected to arise from the fact that heavy expenditure of captured resources in new leaves and roots will be of selective advantage only in circumstances where active foraging gains access to large reserves of light energy, water and mineral nutrients. From this argument we may suspect that competitive dominants will be excluded from habitats in

which productivity is low and resource availability is brief and unpredictable (e.g. light as sunflecks, mineral nutrients as short pulses from decomposition processes or water as occasional rainshowers). In these circumstances conservation of captured resources is of primary significance and dominant plants are likely to be those which owe their status to their capacity to harvest *and retain* scarce resources in a continuously hostile physical environment. In keeping with this prediction, we find that the leaves of plants of unproductive environments tend to be comparatively long-lived, morphologically-implastic structures which are strongly defended against herbivory (Grime 1979; Bryant & Kuropat 1980; Coley 1983; Cooper-Driver 1985).

Stress-tolerant dominants, despite their many common features of life-history and physiology (Grime 1977), are associated with a wide range of life-forms and ecologies. This diversity may be related to the fact that in addition to the numerous lichens, bryophytes, herbs and small shrubs of unproductive biomes (arctic, alpine, arid) and habitats (cliffs, rock outcrops, bogs, heathlands), there are also stress-tolerant trees with slow growth rates and long life-spans which occupy relatively unproductive sites (e.g. Currey 1965).

Implications for succession, stability and diversity

Succession

Theories of plant succession in terrestrial environments have been dominated by concepts relating to life-histories, plant architecture and mechanisms of regeneration (Clements 1916; Egler 1954; Drury & Nisbet 1973; Connell & Slatyer 1977; Whitmore 1982; Finegan 1984). One objective of this chapter is to emphasize that some of the structural changes which we observe in vegetation are confounded with physiological transitions, knowledge of which is exceedingly helpful in understanding the mechanisms controlling species replacements and reactions to particular types of perturbation.

In Fig. 20.3 various familiar successional phenomena are portrayed in an attempt to illustrate the potential of strategy concepts to admit physiological criteria into the study of vegetation dynamics. In each succession diagram the strategies of the dominant plants at particular points in time are indicated by the position of arrowed lines within the triangular model. The passage of time in years during succession is represented by numbers on each line and shoot biomass at particular points is reflected in the size of the circles.

Fig. 20.3f depicts the course of secondary succession in a forest clearing

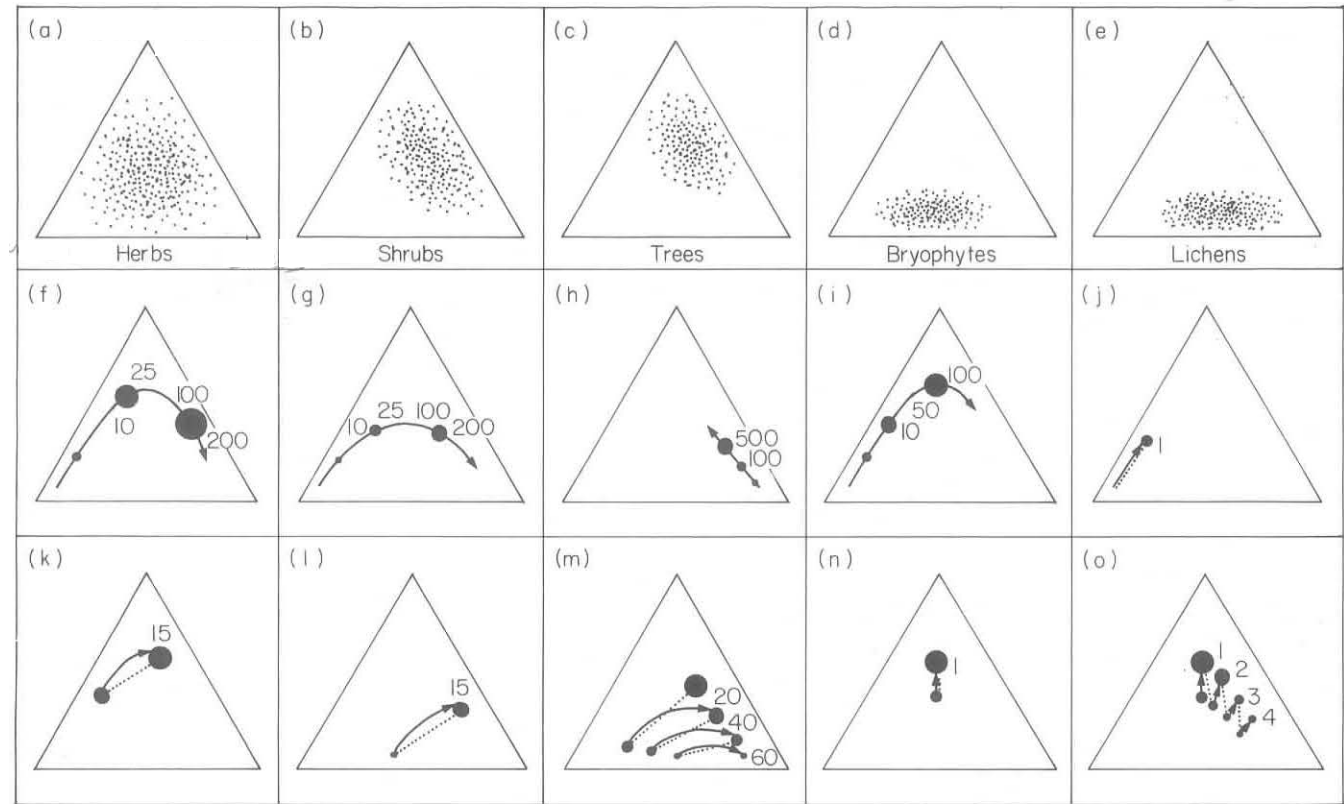


FIG. 20.3 Models describing the strategic range of five life forms (a–e) and representing various successional phenomena (f–o). (a) herbs, (b) shrubs, (c) trees (d) bryophytes, (e) lichens. For a description of the succession diagrams see text.

situated on a moderately fertile soil in a temperate climate. Biomass development is initially rapid and there is a fairly swift replacement of species as the community experiences successive phases of competitive dominance by rapidly growing herbs, shrubs and trees. At a later stage, however, the course of succession begins to deflect downwards towards the stress-tolerant corner of the triangular model. This process begins even during stages where the plant biomass is expanding appreciably and reflects a change from vegetation exhibiting high rates of resource capture and loss, to one in which resources, particularly mineral nutrients, are efficiently retained in the biomass.

In Fig. 20.3g secondary succession is described for a site of lower soil fertility. Here the course of events is essentially the same as that described in Fig. 20.3f except that the successional parabola is shallower and the plant biomass smaller as a consequence of the earlier onset of mineral nutrient limitation of the initial phase of competitive dominance.

Primary succession in a skeletal habitat such as a rock outcrop is represented in Fig. 20.3h. In this case the initial colonists, probably lichens and bryophytes, are stress-tolerators of low biomass and they occupy the site for a considerable period, giving way eventually to small slow-growing herbs and shrubs. This sequence coincides with the process of soil formation and provides an example of the facilitation model of vegetation succession (Connell & Slatyer 1977).

In the examples so far considered plant succession has been interpreted mainly as an interaction between resource availability and the characteristics of established plants. Greater sophistication can be introduced into the models by including circumstances where ineffective seed dispersal or failure in seedling establishment limits access of potential dominants into successional pathways. Fig. 20.3i, for example, describes the common situation (Niering & Goodwin 1962; Kochummen & Ng 1977) in which the development of a dense herbaceous cover prior to the arrival of the propagules of woody species prevents their establishment and strongly delays succession.

The range of models can be extended further to include loops representing vegetation responses to major perturbations. These vary from simple truncation of succession by annual harvesting and fertilizer input in an arable field (Fig. 20.3j) to the cycles of vegetation change associated with coppicing *Fraxinus excelsior* woodland (Fig. 20.3k) or rotational burning of *Calluna vulgaris* moorland (Fig. 20.3l). Where the vegetation of moderately unproductive habitats is subjected to repeated cycles of destruction by burning, browsing or cropping (Fig. 20.3m), the declining mineral nutrient capital of the soil may be expected to bring about a

series of arcs of progressively lower trajectory in successive cycles of vegetation recovery.

Finally, models can be drawn to represent circumstances in which proclimax communities are maintained by orderly sublethal damage to the vegetation. Fig. 20.3h describes a productive fertilized meadow in which the expansion of competitive dominants is restricted by annual mowing. In Fig. 20.3o we see the sequence of events where the meadow is not fertilized and there is a drift towards lower productivity and incursion by stress-tolerant species.

Stability

Reference to some of the essential differences between ruderal, competitive and stress-tolerant dominants, reviewed earlier in this chapter (pp. 414–419) provides the basis for predictions of vegetation stability. These predictions have been discussed (Grime 1979) and tested (Leps, Osbornova-Kosinova & Rejmanek 1982) elsewhere. Here it will suffice to make the essential distinction between resistance to perturbation (low in ruderal and competitive dominants, higher in stress-tolerant dominants) and resilience (highest in the first two, lower in the latter) and to add that the regenerative strategies of plants, particularly those involving the maintenance of persistent banks of seeds or buds within the soil, are a major additional determinant of resilience.

Diversity

Where fast-growing herbs or shrubs with the capacity for clonal expansion are able to exercise competitive dominance it is not unusual to find exceedingly low floristic diversity. Mechanisms which have been proposed to explain the low invasibility of these 'near-monocultures' include intense shading and deposition of litter and it has been suggested already (pp. 416–418) that local resource depletion below ground may be important also. In addition we may suspect that the very dynamic 'foraging' responses of the leaves and roots of competitive dominants creates a highly unpredictable and hazardous environment for smaller plants of narrower niche width. In marked contrast, we may suspect that where vegetation is dominated by stress-tolerant plants, the more predictable matrix of living and dead materials which they provide will allow greater opportunity for other plants to exploit the habitat. This prediction appears to be confirmed by observations of high diversity in mature communities of relatively unproductive forests and grasslands (Holdridge

et al. 1971; Bratton 1976; Furness 1980) in both of which co-existence with stress-tolerant dominants often involves well defined spatial relationships with or attachment to living or non-living surfaces of the dominant plants.

SUBORDINATES

In Fig. 20.1 it is suggested that plants which are incapable of dominance fall into two broad classes. First, there are the plants characteristic of extreme habitats where the intensities of stress or disturbance, or of various combinations between the two, are sufficient to exclude potential dominants. Second, there are subordinate plants which through a variety of mechanisms coexist with dominant plants. As stated in Grime (1979), some 'by virtue of their morphology or phenology, escape the main impact of the stresses generated by the dominant (e.g. vernal herbs beneath deciduous trees) whilst others (e.g. evergreen herbs in woodland) are adapted to tolerate these stresses. Coexistence in certain other plants is achieved by exploitation of areas within the habitat where the environment is locally unfavourable to the dominant. In addition there are subordinate species which owe their presence to microhabitats created by the dominant (e.g. epiphytic angiosperms, ferns, mosses and lichens).'

Complementing the definition of dominance on p. 414, subordination may be recognized therefore as the consequence of those specializations, of many different kinds, which prevent the majority of plants from monopolizing the edaphic and aerial environments. These specializations have morphological, phenological and life-history concomitants and restrict the activity of the plant to part of the micro-environmental mosaic and/or to part of the available growing season.

Fitness of subordinates

The Introduction to this paper questioned whether there were distinct selective advantages associated with playing a subordinate role in communities. Reference to Table 20.1, which identifies the twenty-four most commonly occurring herbaceous plants of the Sheffield region, provides strong evidence that some subordinates (*Cerastium fontanum*, *Heracleum spondylium*, *Plantago lanceolata*, *Poa trivialis* and *Rumex acetosa*) are as widely successful as the most familiar dominants. Clearly many factors determine the fitness of species in an area of varied landscape and vegetation cover. These include genetic variation within and between populations, flexibility in mechanisms of regeneration and capacity to

TABLE 20.1. The commonest herbaceous plants of the Sheffield region. The values tabulated refer to the percentage of 2748 m² samples found to contain the species. Subordinate species are indicated by heavy type

<i>Poa trivialis</i>	22.0	<i>Rubus fruticosus</i> agg.	11.5
<i>Deschampsia flexuosa</i>	20.3	<i>Festuca ovina</i>	11.2
<i>Festuca rubra</i>	19.4	<i>Plantago lanceolata</i>	9.6
<i>Agrostis capillaris</i>	18.3	<i>Cerastium fontanum</i>	9.2
<i>Holcus lanatus</i>	18.1	<i>Elymus repens</i>	9.2
<i>Dactylis glomerata</i>	17.9	<i>Hyacinthoides non-scripta</i>	9.1
<i>Poa pratensis</i>	15.0	<i>Heracleum shondylium</i>	8.5
<i>Arrhenatherum elatius</i>	14.3	<i>Ranunculus repens</i>	8.2
<i>Holcus mollis</i>	12.8	<i>Rumex acetosa</i>	7.9
<i>Chamerion angustifolium</i>	12.6	<i>Lolium perenne</i>	7.8
<i>Poa annua</i>	12.1	<i>Pteridium aquilinum</i>	7.8
<i>Taraxacum officinale</i> agg.	12.0	<i>Mercurialis perennis</i>	7.0

exploit the most commonly-occurring habitats. In the case of common subordinates, however, two additional factors deserve consideration.

(a) Many subordinate species are capable of exploiting a similar niche in a variety of habitats and in association with a wide range of dominants. *Poa trivialis*, for example, appears as a vernal component in eutrophic woodlands, grasslands and marshes with an extraordinarily wide range of dominants including taller grasses, broad-leaved herbs and woody plants.

(b) The reduced morphology and restricted phenology of many of the most successful subordinate species reduces the risk and severity of damage due to factors such as drought, flooding, grazing, mowing and burning. In consequence, populations of subordinates may be expected to show a degree of homeostasis greater than that of the dominants when exposed to fluctuating conditions of climate and management.

Implications for succession and diversity

Succession

Earlier in this paper it has been suggested that it is the interactions of the various kinds of dominant plants with their environments and with each other which provides the main impetus for succession. Against this background it is tempting to regard subordinates as mere dependents or opportunists. This view would be mistaken, however, since there is abundant evidence that subordinate plants often influence the fate of dominant plants. It is generally accepted (p. 421, Fig. 20.3h) that in primary succession relatively inconspicuous plants such as lichens and mosses have

a critical role in soil formation and thus facilitate succession to vegetation dominated by vascular plants. Similarly nitrogen enrichment of the soil through the presence of subordinate leguminous plants could eventually favour one dominant at the expense of another. It is also relevant to point out that in order to invade potentially favourable habitats many of the most effective competitive dominants which appear early in secondary successions (*Chamerion angustifolium*, *Phragmites australis*, *Typha* spp., *Epilobium hirsutum*, *Salix* spp.) depend upon establishment by tiny and extremely vulnerable seedlings. Recent field studies (Hillier 1984; Keizer, van Tooren and During 1985) have shown that selective effects on invading seedling populations can be exercised by bryophytes. In view of this it seems reasonable to suggest that subordinate plants could often play a critical role in succession through their influence upon the colonizing success of various dominants. Selective effects on seedling establishment may arise from the presence of even less conspicuous members of the plant community. This may be illustrated by reference to a recent experiment in which the mortality of seedlings of various herbaceous plants was measured in microcosms in which the soil surface was colonized to various extents by a film of blue-green algae. The results (Fig. 20.4) reveal that there were strong selective effects. Small-seeded species such as *Centaureum erythraea* and *Juncus bufonius* failed completely in circumstances where grasses such as *Festuca ovina* and *Dactylis glomerata* established successfully.

Diversity

Already it has been predicted (p. 422) that in successional communities diversity will be greater where the dominant plants are relatively stress-tolerant and the less dynamic behaviour of the shoots and roots will create microhabitats of sufficient duration for exploitation by subordinate plants. This phenomenon achieves its greatest expression in nutrient-stressed tropical rainforest (Holdridge *et al.* 1971) where even the living leaves of the dominant trees may provide niches for epiphytic subordinates.

It thus appears that in some forests high diversity arises, at least in part, from the presence of numerous relatively stable niches for subordinate plants. Diversity in tropical and temperate forests also, of course, depends upon many additional factors such as the presence of local successional sequences initiated where canopy gaps arise from tree falls.

In grasslands, high densities of subordinate plants are characteristic of species-rich communities, a relationship formalized in the humped-back model (Grime 1973a) which, as shown in Fig. 20.5, can be related directly

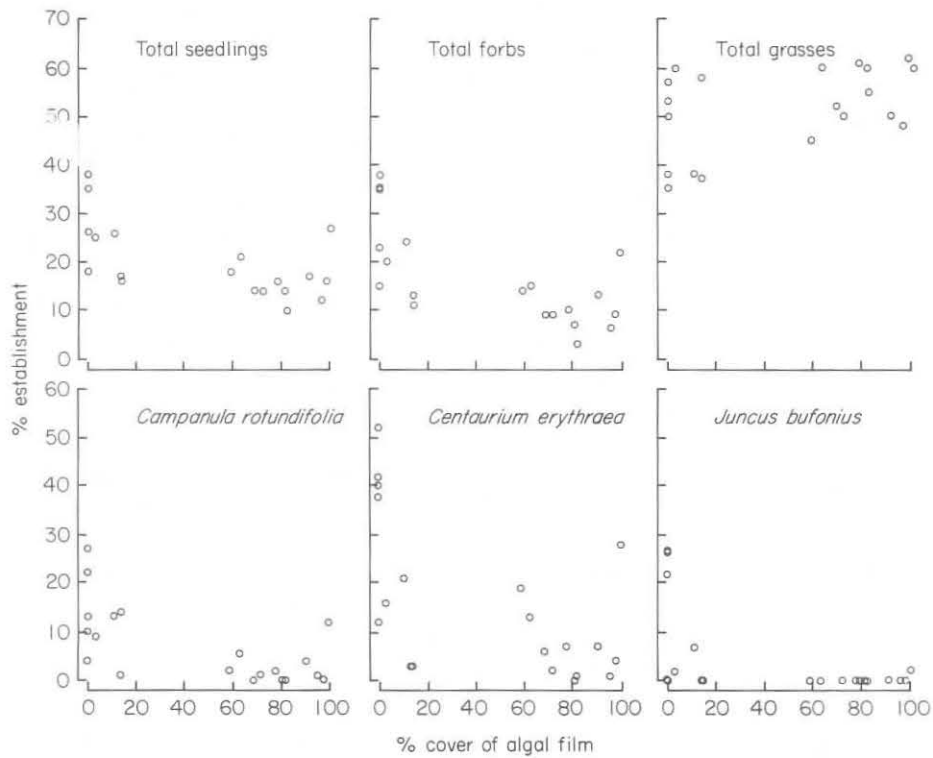


FIG. 20.4 Establishment of seedlings in microcosms varying in percentage cover of the soil surface by an algal film: (a) all species; (b) forbs; (c) grasses; (d) *Campanula rotundifolia*; (e) *Centaurium erythraea*; (f) *Juncus bufonius*.

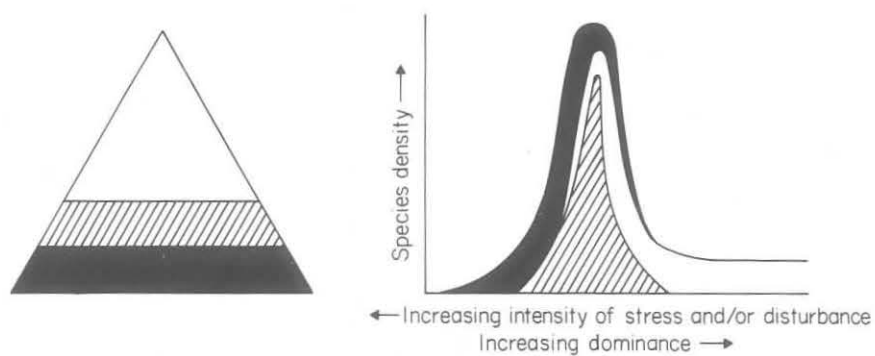


FIG. 20.5 Scheme describing the distribution of three floristic elements in the C-S-R model (left) and in the humped-back model (right). The axes and positions of strategies in the C-S-R model are as in Fig. 20.1a: (□) potential dominants; (■) plants highly adapted to extremely disturbed and/or unproductive conditions; (▨) subordinates.

to the C-S-R model of primary plant strategies. Although the humped-back model has been tested by quantitative studies (Al-Mufti *et al.* 1977), uncertainties remain with regard to the processes which often allow large numbers of subordinate plants to coexist within 'the hump'. As the reviews of Grubb (1977), Grime (1979), Huston (1979), Pickett (1980), and Tilman (1982) make clear, there is considerable diversity of opinion with regard to the relative importance of spatial heterogeneity, vegetation disturbance, regeneration opportunities and specific environmental stresses in the maintenance of species-richness. It seems possible that further penetration into this problem may not be possible by conventional studies in the field. Accordingly, current work on grassland diversity at Sheffield involves experimental manipulation of species-rich microcosms synthesized under controlled conditions.

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